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A conceptual model of spruce beetle population dynamics

L. Safranyik, C. Simmons and H.J. Barclay

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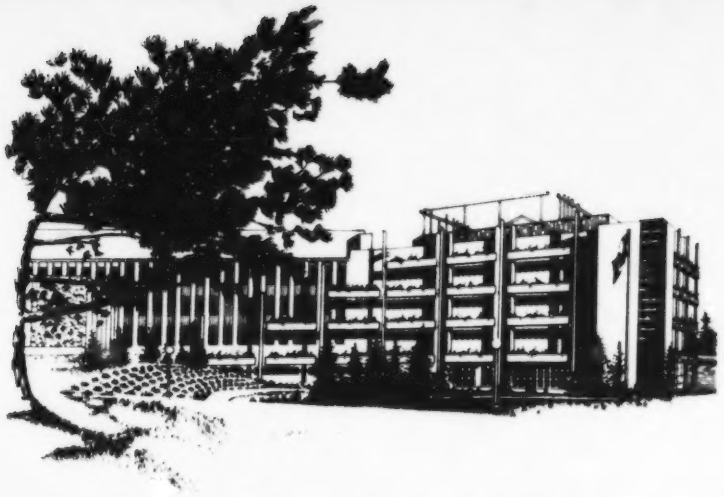

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About the Authors

Les Safranyik

Les Safranyik is a research scientist with Forestry Canada and project leader for research on bark and wood boring insects. His speciality is bark beetle population dynamics and management. Dr. Safranyik received his B.S.F. in 1961, his M.F. in 1963, and his Ph.D. in 1969, all from the University of British Columbia.

Hugh Barclay

Hugh Barclay is a research scientist with Forestry Canada. His specialty is modelling insect population dynamics, especially as applied to pest control. He received his B.Sc. in 1964 from the University of British Columbia, and his M.Sc. in 1973 and his Ph.D. in 1978, both from the University of Victoria.

Clarence S. Simmons

Clarence Simmons, the applied statistician at the Pacific Forestry Centre, advises on the design and conduct of experiments, on the statistical analysis of data, and on the interpretation of results. Dr. Simmons does some statistical analysis himself, using either proprietary software or software that he writes himself, and occasionally he designs and writes non-statistical computer programs for modellers.

Dr. Simmons received his B.Sc. from the University of Reading (England) in 1962, and his M.Sc. and Ph.D. from the University of Guelph in 1966 and 1974, respectively.

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Forestry Canada
Pacific and Yukon Region
Pacific Forestry Centre
506 West Burnside Road
Victoria, British Columbia
V8Z 1M5
Phone (604) 388-0600

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Contents

Abstract/Résumé v
Introduction 1
Spruce beetle biology and habits 1
Model construction 2
1. Structure, time scale, and modelling approach 2
2. The biological model 2
(i) Forest submodel 3
(ii) Tree susceptibility submodel 3
(iii) Insect attack submodel 4
(iv) Beetle population submodel 5
Model testing 6
1. Simulation 6
2. Sensitivity analysis 7
Discussion 9
Acknowledgements 10
Reference 11

Abstract

A forest-based conceptual model of spruce beetle population dynamics was developed based largely on the collective hypotheses, experience, and intuition of the bark beetle research team at Pacific Forestry Centre. Only a limited amount of published and unpublished information, from a population dynamics study of the spruce beetle in central British Columbia, was used in the development of the model. The model provides a means for evaluating the relative importance of a number of factors affecting spruce beetle populations and mortality of spruce from the spruce beetle. Sensitivity analysis indicated that the factors in the model that had the greatest effects on cumulative spruce mortality were forest age, mean July-August temperature, maximum wind speed, winter mortality of beetles, and direct control. High densities of logging residue or windfall were not always followed by increased killing of spruce trees; high densities of susceptible trees were also required for development of outbreaks. This model is useful for illustrating which factors might be important in the development and course of a spruce beetle outbreak.

Résumé

Un modèle conceptuel forestier de la dynamique des populations du dendroctone de l'épinette a été élaboré principalement à partir des hypothèses, de l'expérience et de l'intuition de l'ensemble des membres de l'équipe de recherches sur le scolyte de l'écorce du Centre de foresterie du Pacifique. Seulement un nombre limité de données publiées et inédites provenant d'une étude de la dynamique des populations du dendroctone de l'épinette menée dans le centre de la Colombia-Britannique ont servi à l'élaboration du modèle. Le modéle constitue un outil pour évaluer l'importance relative d'un certain nombre de facteurs agissant sur les populations du dendroctone de l'épinette ainsi que pour déterminer la mortalité des épinettes attribuable à ce ravageur. Des analyses de sensibilité ont révélé que les facteurs du modèle ayant les effets les plus marqués sur la mortalité cumulative de l'épinette étaient l'âge du peuplement forestier, la température moyenne en juillet-août, la vitesse maximale des vents, la mortalité hivernale des dendroctones et les interventions directes. La présence d'une forte densité de résidue d'exploitation et de chablis ne se traduisait pas toujours par une augmentation de la mortalité des épinettes; il fallait qu'un grand nombre d'arbres vulnérables soient présents pour qu'apparaisse une infestation. Ce modèle permet d'illustrer quels facteurs pourraient jouer un rôle important dans l'apparition et l'évolution d'une infestation du dendroctone de l'épinette.

Introduction

The spruce beetle (*Dendroctonus rufipennis* (Kirby)) is native to the spruce (*Picea* sp.) forests of North America. In British Columbia, it is the most destructive pest of mature spruce forests (Cottrell 1978). In 1972, a multidisciplinary research project was developed at the Pacific Forestry Centre with the main objectives of discovery, development, and promotion of principles, techniques, and management guidelines to reduce losses from wood-boring and phloem-feeding insects. The major research effort was initially directed at the spruce beetle. A theoretical model of spruce beetle dynamics was built in an attempt to evaluate the relative importance of a number of factors that were thought to affect spruce beetle populations and the damage caused by them.

The model is theoretical (or conceptual) as only a limited amount of data was used in its development; model structure and interrelations among variables are based on collective hypotheses, experience, and intuition developed and tested in consultations among the members of the research team (see Acknowledgements).

The model was built in an interactive mode and allows an evaluation of the relative effects of a number of biological factors, including tree and stand factors, climatic variables, and management practices on spruce beetle populations and damage levels. The objectives of this paper are to describe model development and structure, and to evaluate the performance of the model.

Spruce beetle biology and habits

The spruce beetle is principally a pest of mature forests. Outbreaks can develop and persist in large pole and immature stands but usually develop in mature or overmature stands (Wygant and Lejeune 1967). In western Canada there are periodic severe outbreaks in white spruce (*Picea glauca* (Moench) Voss) and Engelmann spruce (*P. engelmannii* Parry) forests. Normally, the beetle attacks windfalls, logging slash, and injured trees (Cottrell 1978). During epidemics, however, apparently healthy trees may be killed over large areas (Safranyik *et al.* 1983).

Outbreaks usually develop during hot, dry growing seasons and all known outbreaks have occurred following large-scale windfall or large accumulations of man-made slash. However, either or both of these conditions does not invariably result in an outbreak; these conditions appear to be necessary but not sufficient in themselves for development of outbreaks (Safranyik *et al.* 1983). The flight and attack period and the length of the life cycle are governed by temperature (Safranyik 1985). The beetles emerge from May through August, but peak flight normally occurs in June. Upon locating a suitable host, the female beetles bore through the outer bark and commence construction of egg galleries in the inner bark. Following the initiation of boring, the female beetles begin producing population-aggregating pheromones[1] which, in combination with host volatiles, attract beetles of both sexes to the host. Depending on the size of the beetle population, the density and spatial distribution of host materials, and temperature conditions, colonization (mass attack) of individual hosts may take a few days to three weeks.

The egg galleries run parallel to the grain and average about 13 cm in length. About 60 to 80 egg galleries/m^2 are normal near breast height in attacked trees. Mating takes place in the egg galleries. Normally, three to four groups of 20 or more eggs are laid in grooves cut along the sides of the egg gallery, resulting in a total of 80 to 100 eggs per egg gallery. During warm, dry summers parent beetles may re-emerge to attack new hosts. Typically, standing trees are infested up to a height of 12 to 15 m on the bole but windfalls and felled trees may be infested for their full length to the point where the bole diameter is 5 to 7 cm.

The life cycle varies from 1 to 3 years (Schmid and Frye 1977). In most areas, the 2-year cycle predominates, with various proportions of the brood developing on a 1-year cycle. Larval diapause in the fourth instar is induced when larvae are subjected to cool temperatures during early development (Dyer and Hall 1977). On a 2-year life cycle, the brood overwinters once as larvae and once as adults. The 3-year cycle is rare and confined to cool, shady locations. Regardless of the length of the life cycle, diapause is mandatory for young beetles; that is, they must overwinter once as adults in order to reproduce. In late summer and early fall, some of the young adults emerge from standing trees, fall or crawl to the ground, and re-enter the trees near the base in order to hibernate. The proportion of beetles that drop to the bases of trees to hibernate varies considerably from year to year.

The attacking beetles of both sexes carry associated blue stain fungi into the tree which are sloughed off during construction of galleries. In suitable live trees, these fungi quickly penetrate ray and other living cells in both phloem and sapwood. The spread of the fungi

[1] An aggregating pheromone has not been isolated from the spruce beetle, but its presence has been demonstrated with virgin females boring in spruce bolts (Dyer and Taylor 1968). The synthetic pheromone frontalin (1,5-dimethyl-6,8-dioxabicyclo[3.2.1.]octane), in combination with the host component alpha-pinene, is effective for aggregating spruce beetles on host material (Dyer and Chapman 1971).

around the tree is mainly due to larval mining. If the blue stain fungi successfully colonize the living cells, they kill the tree. The killing of living cells by the fungi enhances brood establishment and survival by preventing the production of resinous substances. Resin production is the principal resistance mechanism of trees against attack by the bark beetle-blue stain fungi complex (Safranyik *et al.* 1983). The ability of trees to produce resin in response to injury generally declines with age following maturation (Shrimpton 1973). Also, resin production is adversely affected by stress factors such as hot, dry periods during the growing season coupled with below-normal precipitation (Puritch and Mullick 1975; Shrimpton 1978).

During outbreaks, which normally last about 4 years, proportionately more larger diameter trees are attacked and killed (Swaine 1931; Werner and Holsten 1983; Safranyik *et al.* 1983). The most susceptible stands appear to be those growing on good sites at low elevations (Knight *et al.* 1956), especially when there is a large proportion of spruce in the overstory (Schmid and Hinds 1974) and the spruce has reduced radial growth (Hard *et al.* 1983; Safranyik *et al.* 1983). Safranyik (1985) showed that the incidence of infestations was directly related to site quality, stand age, and the spruce component of stands, and inversely related to elevation.

When spruce beetle populations are low, a number of factors interact to restrain the potential of such populations to increase. These factors include climatic effects (directly on the insect and indirectly through the tree), relations with the blue stain fungi and the tree, predation, parasitism, and disease. The relaxation of some of these factors may permit outbreaks to develop.

Model Construction

The model was written in FORTRAN IV and presently runs on a Vax 8650 under VMS. Since the model was created in the mid-1970's, imperial units were used, and are still used in the present version. The imperial units have been converted to metric units for the graphical output presented in this report.

1. Structure, time scale, and modelling approach

The simulation model is composed of two sections: the biological component, made up of 14 subroutines and the main program; and the nonbiological component, made up of 12 utility subroutines. The nonbiological subroutines are programs that control input, output, and interactive simulation. The biological subroutines

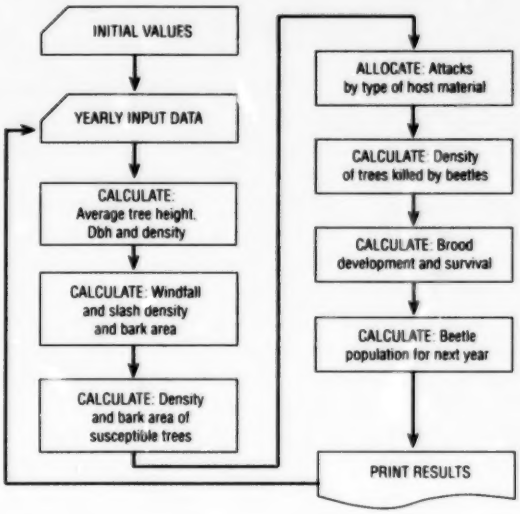

INITIAL VALUES
YEARLY INPUT DATA
CALCULATE: Average tree height, Dbh and density
CALCULATE: Windfall and slash density and bark area
CALCULATE: Density and bark area of susceptible trees
ALLOCATE: Attacks by type of host material
CALCULATE: Density of trees killed by beetles
CALCULATE: Brood development and survival
CALCULATE: Beetle population for next year
PRINT RESULTS

Figure 1. Simplified flow chart of the spruce beetle model.

simulate basic forest variables, the interaction between the spruce beetle and its host, and the population biology of the beetle. Some field data obtained as part of the spruce beetle population study during the period from 1973 to 1975 and some other published data, as described below, were used for development of the various empirical relationships among biotic and abiotic factors. In most cases, however, both the algebraic form and the parametric values of these relationships were deduced from the collective experience and intuition of the research team.

The model is coded to yield an interactive simulation. Simulation is done for an even-aged, unmanaged forest situation, and follows an annual cycle (Figure 1).

2. The biological model

In developing this model, we assumed that factors that have major effects on beetle establishment and survival (the incidence of windfall and logging residue, and the susceptibility of living trees to attack) are the major determinants of changes in beetle population and damage levels. These factors are discussed briefly in the description of the submodels.

The biological component consists of four parts: i) a forest submodel, ii) a tree susceptibility submodel, iii) an insect attack submodel, and iv) a beetle population submodel. A stand of spruce is specified in terms of area, site quality, age, proportion of spruce, decay condition, soil moisture status, and logging history. An index of tree susceptibility is generated based on climatic factors as well as tree and forest characteristics. Beetles are introduced to attack available slash, wind-

falls, and susceptible trees, and a beetle population is generated for attack the following year (Figure 1).

(i) Forest submodel. The purpose of the spruce forest model is to generate host material for the insect. Emphasis was placed on modelling those forest characteristics that were judged to have important effects on the establishment, reproduction, and survival of the beetle — age, height, diameter, density, bark area, and density of spruce windfall and slash. Average tree height (Figure 2), diameter (Figure 3), and density at the beginning of the simulation period are determined separately for each of three growing sites as functions of age, based on data in Stanek (1966) and the University

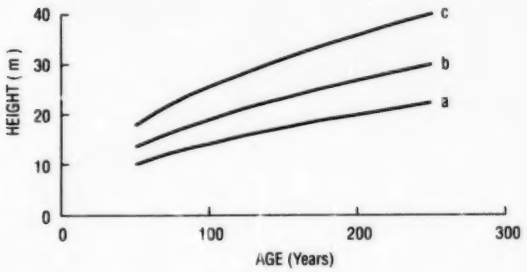


Figure 2. Relationship between stand age and average tree height on poor (a), medium (b) and good site (c).

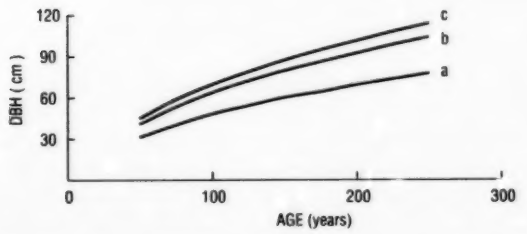


Figure 3. Relationship between stand age and the average dbh of trees on poor (a), medium (b) and good site (c).

of British Columbia Forestry Handbook (1971). Average tree density is adjusted yearly for windthrow and trees killed by spruce beetles. In computing bark area, it is assumed that trees have conic shapes and that infested height increases with dbh (Massey and Wygant 1954). When the simulated forest is composed of more than one growing site and different proportions of spruce (by number of stems) on each site, weighted averages of tree height, diameter, and density are computed for the entire forest.

Although the proportion of trees attacked by spruce beetles during an epidemic is related to tree diameter (Balch 1942; Safranyik 1985), dbh distribution was not modelled for the following reasons: a) stand mortality is related to both the pre-outbreak stand density and dbh of spruce (Safranyik 1985); and b) it was assumed, for simplicity, that the beetle kills the forest in patches and the average diameter of the residual stand is not affected.

Logging may be simulated by specifying the logged area, the length-to-width ratio of the cut, average stump height, and the year of the cut (or the first and last years of a period and an interval). The relationship between breast height diameter and stump height diameter of cut trees is determined as in Alemdag and Honer (1977). Bark area of an individual stump is calculated as the surface area of a cylinder with height and diameter equal to average stump height and average stump diameter. The bark area of logging residue susceptible to attack (exclusive of stumps) is made proportional to stump bark area, based on data from areas in the Naver Forest, about 50 km southeast of Prince George, British Columbia, logged during 1973-75.

Windthrow density is determined separately for wet soils and for well-drained soils inside the forest as well as along forest edges. Windthrow density inside the forest (J.A. Turner, Forestry Canada, Pacific Forestry Centre, Victoria, personal communication) is expressed as a function of maximum wind gust for the year, mean wind speed for the area, average tree height, the proportion of spruce stems with visible decay, and the change in the average density of live trees during the previous 3 years (Figure 4). Forest edge is defined as a strip of forest 20 m deep bordering openings that were created within the 4 years preceding the simulation year. Along forest edges, the length-to-width ratio and the area of the logged portion as well as estimates of the relative susceptibility to windthrow of forest edges of various ages (Alexander 1964, 1967) are used for calculating windthrow density. In calculating the bark area of wind-felled trees it was assumed that 75% of the total bark area is attacked regardless of beetle population level.

(ii) Tree susceptibility submodel. For each year of simulation, this submodel generates the probability of a spruce tree being susceptible to attack by spruce beetles on wet and well-drained soils. This model also generates the density of trees susceptible to spruce beetle. All climatic and stand variables used with effects on tree susceptibility can be varied simultaneously or individually.

The probability of a tree being susceptible to spruce beetles in a given year was expressed as a function of stand age greater than 60 years, and the interactions among the following variables: windfall density; relative deviation in July-August average temperature during the previous year from the long-term average July-August temperature; and relative devia-

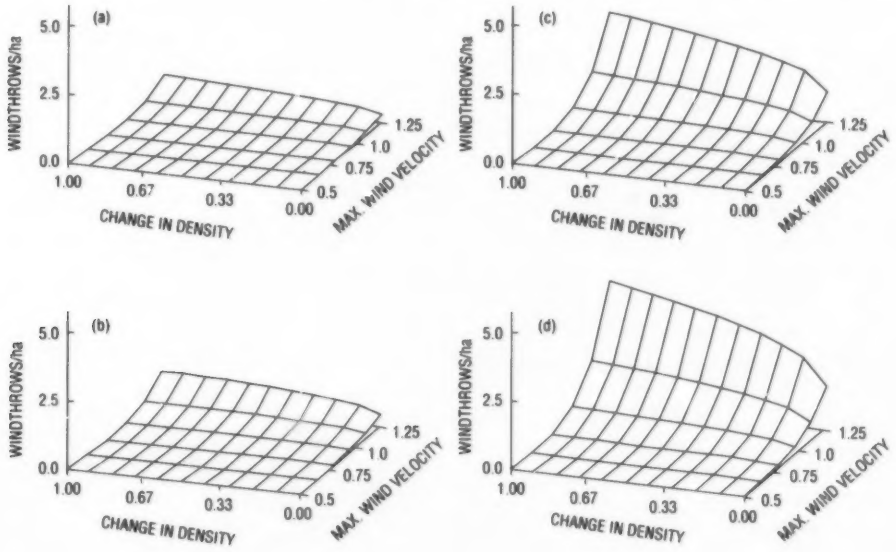


Figure 4. Simulated number of windthrown trees per ha on well drained soils as a function of maximum wind gust velocity and proportional change in the density of live trees during the past 3 years for various combinations of average tree height in metres (H) and the proportion of trees with visible root or basal decay (R). These results are for a mean wind speed of less than 16 km/hr. a) H=15, R=0; b) H=30, R=0; c) H=15, R=0.5; d) H=30, R=.5. The curves were all generated from the general equation:

$$LDX = 0.0184\,(1 + 2\sqrt{D})(1 + 20R^{3})\sqrt{H}\,W^{\wedge}$$

where LDX is windthrown trees per ha, D is change in live tree density during the past 3 years expressed as a proportion of live tree density for the current year, and W is maximum wind gust velocity (km/min.).

tion in May-June precipitation of the previous year from the long-term average May-June precipitation (Figure 5). Increase in host susceptibility with age, especially past the culmination of mean annual increment and the attainment of maximum density, has been observed for lodgepole pine attacked by the mountain pine beetle (Shrimpton 1973; Safranyik *et al.* 1974). Susceptibility of spruce trees to attack by the spruce beetle also increases with stand age (Safranyik 1985). Windfall density was included in the submodel for tree susceptibility because it was assumed that, following heavy winds that uproot trees, the fine root systems of at least some of the standing trees will be damaged and their ability to absorb water and nutrients will be reduced (Safranyik *et al.* 1983). May-June precipitation and July-August average temperature were included into the submodel based on the assumption that reduced precipitation at the beginning of the growing season combined with higher than average summer temperatures would reduce tree growth and hence the resistance response of trees the following year. As well, such weather conditions tend to increase the incidence of brood development on a 1-year life cycle, and hence the rate and concentration of attacks. Both of these factors increase the success of the attack. Spruce beetles tend to attack trees that grow slowly (Hard 1985). Thomson and Shrimpton (1984) showed that very low precipitation levels in some or all of the months from May to August were associated with periods of reduced growth of lodgepole pine and peak growth often occurred when weather conditions throughout the growing season were close to the long-term average. Soil moisture deficit in the late spring and early summer had the greatest inhibiting affect on growth of white spruce in Canada (Fraser 1973).

(iii) Insect attack submodel. This submodel generates the following information: (a) the proportions of the searching female beetles that will attack slash, windfall, and live trees; (b) the proportion of the susceptible trees that will be attacked; (c) the proportion of attacked trees that will die; (d) the density of trees killed by spruce beetles; (e) attack densities per unit bark area in windfall, slash, and live trees; and, (f) loss of beetles during the flight period.

Insect attack is simulated only in forests older than 80 years and with average dbh of spruce greater than

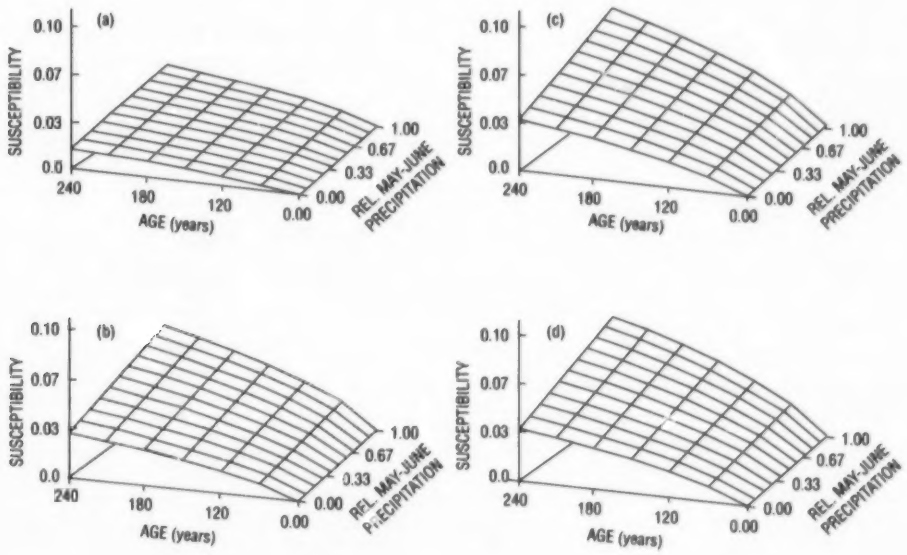


Figure 5. Simulated proportion of trees susceptible to spruce beetle attack on well drained soil (*SUSTD*) as a function of stand age (*A*), average DBH, windfall density (*RL*), and relative deviation in May-June precipitation (*RM*).

(a) DBH = 23 cm, windfall density = 0.25/ha
(b) DBH = 46 cm, windfall density = 0.25/ha
(c) DBH = 23 cm, windfall density = 2.5/ha
(d) DBH = 46 cm, windfall density = 2.5/ha

These curves were all generated from the general equation:

$$SUSTD = (0.05/300)(A\text{-}60)(1+RM)(1+0.08\,RL)DBH/[3.0\sqrt{(A\text{-}15)}]$$

20 cm. The amount of suitable bark area per hectare (slash, windfall, and live trees combined) chosen as the threshold for beetles to establish in a simulated forest was 2.5 m^2/ha. During the first year of infestation, an average density of 12 females/ha is assumed to be established.

The proportions of the spruce beetle population attacking windfall, slash, and living susceptible host trees can be varied externally by changing their "trap efficiency" indices. Trap efficiency defines an area of attraction (a_i) relative to the total simulated forest area, for each of the three types of host materials such that

$$(\sum_{i=1}^{3} a_i = 1).$$

The proportion of susceptible trees attacked, the density of trees dying (Figure 6), and attack density per unit bark area are expressed as functions of the size of the attacking beetle population, of the relative availability of the three types of hosts, and of tree susceptibility. Maximum attack densities of 250/m^2 (for slash and windfall) and 100/m^2 (for live trees) were assumed. All female beetles will establish attacks when average attack density is 60 or fewer per m^2; at attack densities greater than 60 and less than the maximum, the proportion of female beetles that will establish attacks is inversely proportional to attack density. Those beetles that were attracted to slash but could not make attacks search to attack windfall, and those beetles that could not attack either of these hosts will search to attack live trees. The beetles that could not attack any of the three types of hosts are assumed to have died or to have dispersed from the simulated area. The proportion of female beetles that did not make attacks is calculated for each simulation year.

(iv) Beetle population submodel. Separately for the three types of host material, this submodel generates the following information: a) eggs per unit length of egg gallery, b) average egg gallery length, c) egg density (eggs per unit area of bark), d) population quality, and e) the proportion of the brood that develops on a 1-year life cycle. It also generates, separately for the first and second years of the life cycle, the following information: survival of brood through summer; mortality from competition, insect parasites and predators,

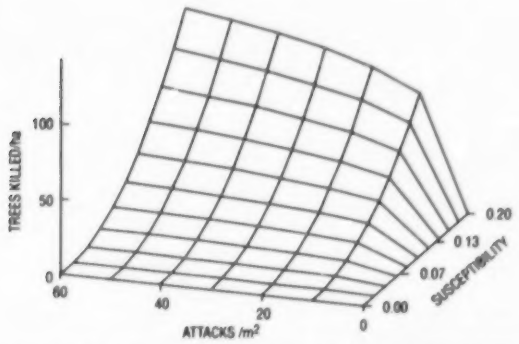


Figure 6. Simulated numbers of trees killed per hectare per year from spruce beetle attacks as a function of average attack density per m^2 (*AT*) and tree susceptibility (*SUSTD*). This surface was generated by the equation:
Trees killed/ha = (0.3528) [$\sqrt[4]{(AT)}$ x *DENSN* x $25SUSTD^2$]
where *DENSN* = density of live spruce (held at 125/ha)

woodpecker predation, low temperatures, and host factors; total beetle population for the stand; and the proportions of the beetles emerging from slash, windfall, and standing trees. The number of eggs per cm of egg gallery (7.0) was estimated from data in Massey and Wygant (1954), and the relationship between average egg gallery length and attack density was estimated from unpublished data of E.D.A. Dyer, Pacific Forestry Centre, Victoria.

We assumed that population quality is a measure of the effects of brood density and host factors on the fecundity of the female adult beetle. Attack density is an index of competition among individuals for food and space as well as a main determinant of attack success in live trees. Population quality for each beetle generation was therefore modelled as a function of attack densities in the current and preceding generation. The numerical values of the population quality index generated vary from 0.1 to 1.9 with 1.0 designating "normal" quality. Population quality can also be given arbitrary fixed values for the simulation period to test its effect on the beetle population and the numbers of trees killed by them. The effects of eggs per cm of egg gallery can be tested in a similar manner; this enables us to test ideas on the use of chemicals, such as those which affect yolk deposition and fertility, for manipulating beetle populations. Chemical control of the insect in the adult stage is simulated by "killing" a portion of the population from the previous year, prior to attack. Available inputs are the years in which chemical control is applied (or the first and last year and an interval), and percent adult mortality.

Only the 1- and 2-year life cycles were modelled. The length of the life cycle was determined by the relationship between temperatures during the young larval stages (assumed to occur during July and August) and the onset of diapause in the fourth larval instar (Dyer and Hall 1977).

Brood survival to the end of the first summer (S_1) is calculated as $S_1 = 1 - (M_c + M_p - M_c M_p)$ where M_c is brood mortality from competition, and M_p is mortality from insect predators and parasites. M_c was modelled as a function of the diameter of the host material and egg density in slash and windfall, and as a function of host susceptibility, host diameter, and attack density in live trees. M_p was assumed to be a constant proportion (5%) of M_c. There is insufficient knowledge of the effects of insect predators and parasites (Schmid and Frye 1977) other than that they collectively cause little mortality. The effects of nematodes, mites, and disease on egg production and survival were not modelled.

Winter survival was modelled as a function of yearly minimum temperatures and was based on reported effects of low temperatures on beetle survival (Massey and Wygant 1954). Mortality from woodpeckers was modelled as a function of brood density only (Knight 1958; Koplin and Baldwin 1970). A maximum mortality of 40% from woodpecker predation was assumed. Also, the probabilities of an insect dying from low winter temperatures or from woodpecker predation can both be set externally to a fixed value for the duration of the simulation period. Mortality during the second year of the life cycle is modelled in a similar manner to that described above for the first year of the life cycle.

Model Testing

Weather data from one location over a period of 57 years are built into the program. These data, whether modified or not, are supplied to the model at the start of each simulation. Each pass through the main loop of the program simulates a year.

1. Simulation

In evaluating the performance of the model, emphasis was placed on the long-term effects of changes in the numerical values of some key parameters on the cumulative density of trees killed by the spruce beetle. These key parameters (e.g., site quality, percentage of spruce in the stand, logging, windfall, beetle productivity and population quality, and killing (control) of adult beetles) were selected based on published information and experience. Some relationships among these variables were also examined. These simulations are based on weather data from Prince George, British Columbia for each year between 1917 and 1973. Prince George had

long continuous weather records and it is located in an area that historically has suffered repeated large-scale outbreaks. Some of the more important results are as follows:

(1) Both site quality and the percentage of spruce strongly affect the density of spruce killed by spruce beetles (Figure 7).

(2) In mature stands, low beetle population levels tended to occur during years when a high proportion of the population emerged from the wind-felled trees (Figure 8).

(3) A high density of susceptible trees is required for the development of an outbreak.

(4) There was a direct but weak relationship between the density of attacked trees and the percentage of beetles developing on a 1-year life cycle (Figure 9). High slash or windfall density (Figure 10) and high pre-outbreak beetle numbers are apparently neither necessary nor a sufficient condition for an outbreak in live trees.

(5) Brood productivity in logging slash is generally lower than in windfall or standing trees. However, as the density of windthrow is high on the cut edges compared to that inside the stand, some combinations of edge windthrow density, brood survival, and stand susceptibility will cause a local outbreak (Figure 11).

(6) Changes in the numbers of eggs laid per cm of egg gallery have strong effects on beetle population size but only moderate effects on the density of killed trees (Figure 12).

(7) Killing 95% of the adult beetles through applied control two or three times at intervals of 2 to 3 years at the beginning of an outbreak results in moderate savings in live trees (Figure 13).

(8) Peaks of simulated beetle abundance for a 57-year period generally correspond to the periods of known and locally remembered spruce beetle outbreaks in central British Columbia (Figure 14).

The simulated effects of some of these variables, such as logging residue, windthrow, and tree susceptibility, on tree mortality caused by the spruce beetle reinforced our previous thinking regarding their roles in spruce beetle population dynamics.

2. *Sensitivity analysis*

A parameter sensitivity analysis is included in the simulation program. This systematically varies the values

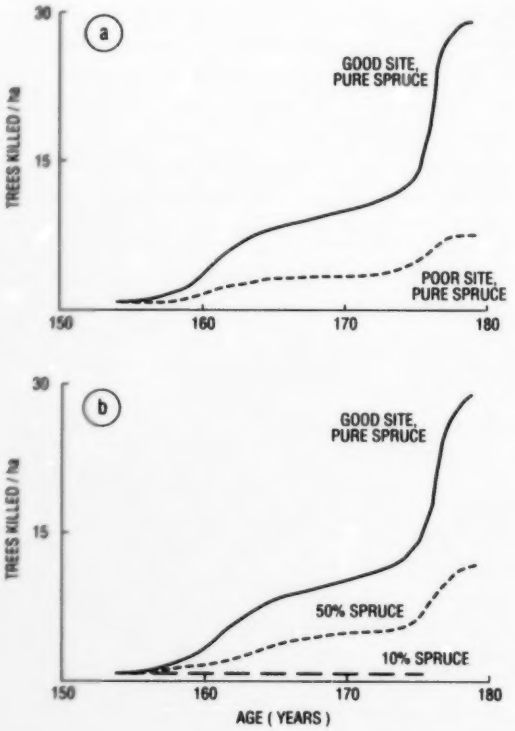
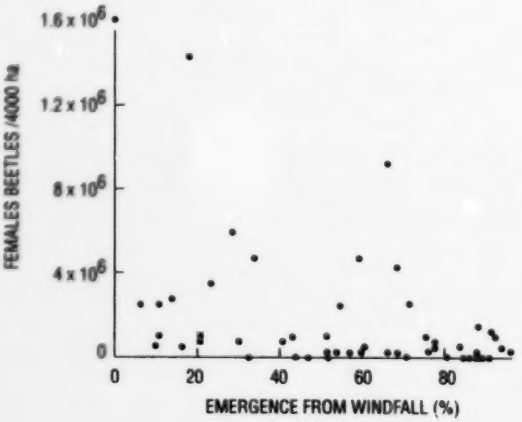


Figure 7. Simulated effects of (a) site quality (using pure spruce on a good site and on a poor site) and (b) spruce composition (using a good site) on cumulative density of trees killed by spruce beetles in a 4000-ha stand during a 30-year period. The stand was 150 years old at the start of the simulation.



of each of the parameters one at a time. In cases where the default value was non-zero, the parameter was varied from 50% of the default value up to 150% of the default value in eleven steps; in cases where the default value was zero, the parameter was varied over a reasonable range. The final values of each of the variables (or, in some cases, the accumulated values over the length of the run) are output to a file for subsequent graphing and inspection. These values are graphed against the value of the parameter being varied. Two variables were selected as being of particular interest to foresters, and these are shown in Figure 15. The variables chosen are (a) the total number of female beetles produced over a 20-year run, and (b) the cumulative number of dead trees per hectare resulting from beetle attack. These are graphed against the following natural and control parameters: the age of the stand at the start of the simulation, the area of the stand, the proportion of the beetles attacking windfall, the proportion of the area that is a dry site, the amount of rain in May, the amount of rain in June, the mean temperature in July and August, the maximum wind velocity, the proportion of trees with visible decay, eggs per unit length of gallery, winter mortality, beetle quality, the proportion of beetles that die from woodpecker predation, the proportion of beetles killed through direct control, the area of spruce forest cut each year, and the length-to-width ratio of the cut.

Of these parameters, the proportion of the area that is a dry site and the length-to-width ratio of the cut had virtually no effect on either the total number of females produced or cumulative mortality over a 20-year run. Of the remaining parameters, the amount of rain in May and in June and the area of spruce forest cut each year had relatively little effect on either the total number of females produced or the cumulative mortality over a 20-year run. The parameters with the strongest effect on the total number of females produced or the cumulative mortality over a 20-year run were the age of the stand at the start of the simulation, the mean temperature in July and August, the maximum wind velocity, winter mortality, and the proportion of beetles killed through direct control. In addition, the total number of females produced in a 20-year run was strongly affected by the area of the stand, the proportion of beetles attacking windfall, the number of eggs per unit length of gallery, and the quality of the beetles. None of the important parameters affected the cumulative mortality over a 20-year run more strongly than they affected the number of females produced over a 20-year run. Since tree deaths are mediated primarily by beetles and since most of the parameters affect the beetles more directly than the trees, it appears that there are buffering factors in the system whereby the production of beetles is not translated directly into tree deaths. The factors that most strongly affected tree deaths were the age of the stand at the start of the simulation, the mean temperature in July and August, and the maximum wind velocity; each of of these factors affected cumulative tree deaths by several orders of magnitude over the 50-150% range of the parameter being varied. Of these factors, only the age of the stand is under any degree of control by the forest manager.

Of the parameters under direct control by the forest manager, the age of the stand is the most important, followed by the proportion of beetles killed by direct control. In addition, winter mortality and woodpecker activity show promise as control agents if either could be manipulated.

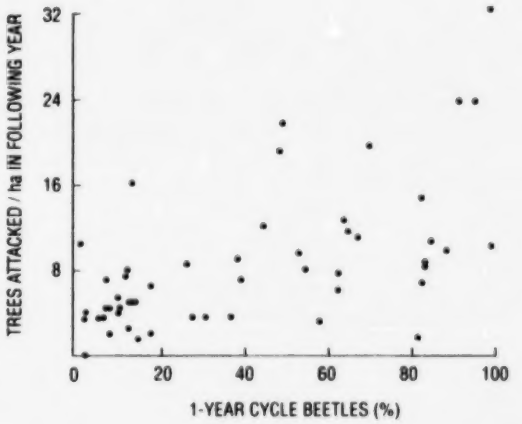


Figure 9. Relationship between the simulated number of trees attacked per hectare per year and the percentage of spruce beetles that developed on a 1-year life cycle during the previous year in a 4000-ha mature spruce forest during a 57-year period. The stand was 150 years old at the start of the simulation.

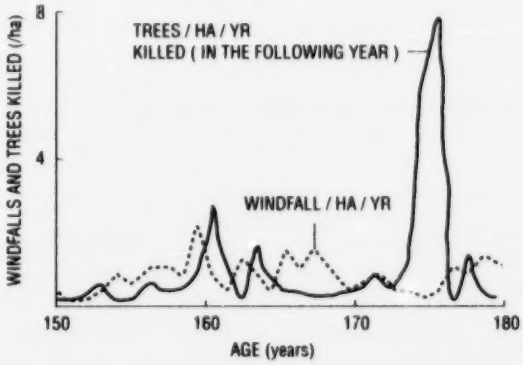


Figure 10. The simulated number of windthrown trees per hectare and the number of spruce trees killed by spruce beetles per hectare the following year in a 4000-ha mature spruce forest over a 30-year period. The stand was 150 years old at the start of the simulation.

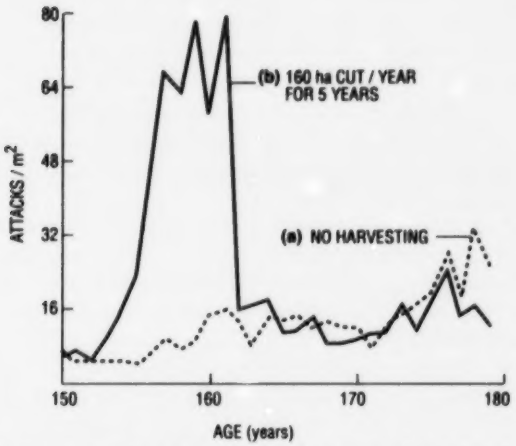


Figure 11. Simulated number of attacks per m^2 in infested trees in a 1250-ha mature pure spruce forest over a 30-year period (a) without harvesting and (b) with clear-cutting one 160-ha block of forest each of the first 5 years of simulation.

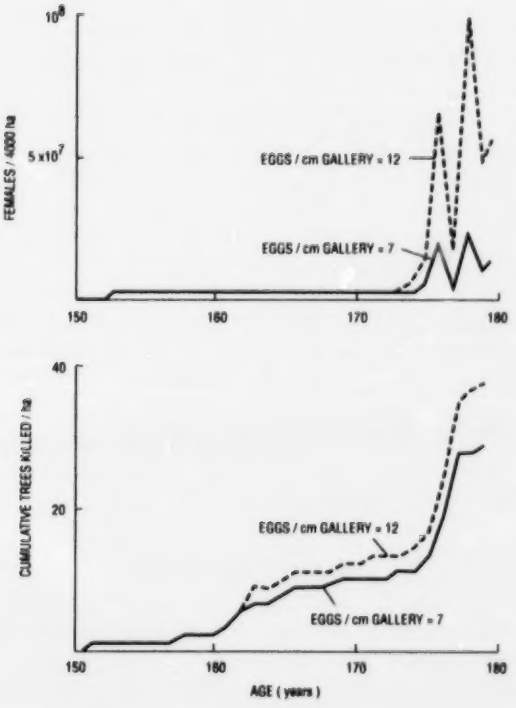


Figure 12. Simulated relationship between forest age and (a) the number of female spruce beetles in a 4000-ha mature forest, and (b) cumulative density of killed spruce trees at two egg densities. Forest age was 150 years at the start of the simulation.

Discussion

The foregoing general analysis indicates that qualitatively, at least, the main characteristics of the interactions between the host and the beetle (such as host susceptibility, windthrow history, and site quality effects on mortality caused by the beetle), and changes in beetle numbers through time (Figure 14) appear to have been simulated reasonably well by the model. As tree death is mediated directly through attacks by female beetles, it is not surprising that the size of the female population was the most important single variable affecting tree mortality. Consequently, any variable that had a strong effect on beetle population size (e.g., density of eggs per unit length of egg gallery length, proportion of females that attacked windfelled trees, beetle quality, proportion of beetles killed by direct control, and winter mortality) was also a major determinant of tree mortality. Other variables that had strong effects on tree mortality were those that influenced both host availability (such as host susceptibility and bark area of susceptible trees) and beetle development and survival (such as age of the trees, maximum wind velocity during the year, average July-August temperature, site quality, and spruce component of the forest). As a consequence of these relationships, high beetle populations did not invariably result in outbreaks and high level of tree mortality. For example, the proportion of beetles attacking windfelled trees had a strong direct effect on the size of adult beetle population, but years with high densities of windfelled trees and large beetle populations emerging from such host materials were not always followed by an outbreak in live trees.

The main results from the simulation runs support experimental observations. Safranyik *et al.* (1983) found that yearly population size of the spruce beetle over a 7-year period in an 831-ha mature forest in central British Columbia varied directly with percent emergence from windfall inside the stand, but not with percent emergence from windfall along stand edges or from logging residue. The year of peak population size coincided with the emergence of the highest percentage of 1-year cycle beetles and was preceded by 3 years of high windfall density. Even though a high density of trees were attacked, most of the attacks were unsuccessful, mainly due to low tree susceptibility. The most severe outbreak on record in central British Columbia, from 1961 to 1963, was preceded by extensive windfall and coincided with depressed incremental growth (Safranyik *et al.* 1983) and summer temperatures hot enough to allow most beetles to develop on a 1-year life cycle (Dyer and Hall 1977). The incidence of infestations and long-term losses from the spruce beetle are strongly and directly related to stand age, site quality, percent host

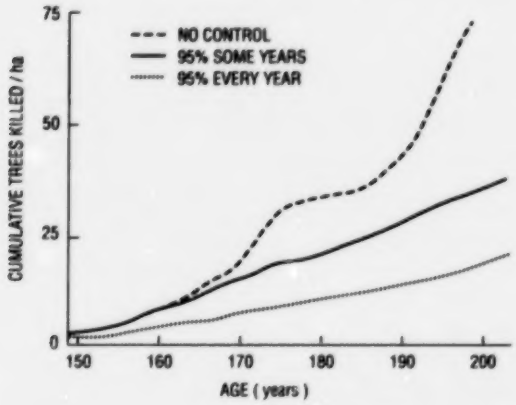


Figure 13. Simulated relationship between cumulative density of killed spruce trees and stand age at three levels of killing (control) of adult spruce beetles in a 4000-ha mature spruce forest during a 57 year period. The three levels of killing were the following: (a) no control, (b) 95% of the beetles killed in the pre-outbreak years 25, 26, 42, 45, 49 and 52, and (c) 95% of beetles killed every year.

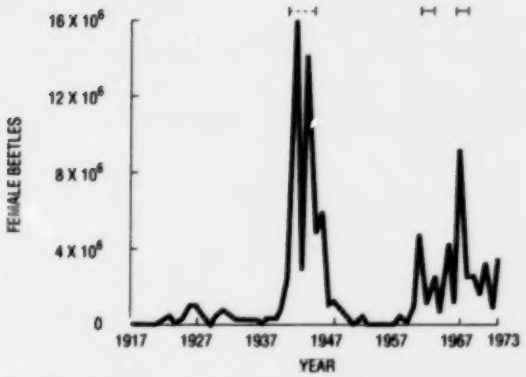


Figure 14. Simulated number of female spruce beetles in a 4000-ha mature spruce forest during a 57-year period and the documented (solid horizontal lines) and locally remembered (broken horizontal line) beetle outbreaks in central British Columbia.

composition and inversely related to elevation (Safranyik 1985). Elevation can be used as an index of temperature conditions for brood development and survival.

Although the sensitivity analysis indicated the area harvested and the shape of the cutblock had little effect on beetle populations and tree mortality, and beetle production in logging residue did not vary with the size of the overall population (Safranyik *et al.* 1983), in some years a large portion of the beetle population may develop in this host material. Consequently, logging residue may be a precursor of a local outbreak.

Decline in beetle vigor and egg deposition rate have been associated with the decline of spruce beetle populations and tree mortality (Knight 1969; McCambridge and Knight 1972). Although beetle vigour (population quality) was modelled only in terms of brood density, the model indirectly incorporates other density-related effects such as incidence of disease and some natural enemies such as mites and nematodes in the adult population.

An unexpected result from simulated control by killing a fixed percentage of the adult beetles was that killing as much as 80% of the adults annually (prior simulation, not shown) resulted in a modest reduction in long-term tree mortality. Similar reductions could be obtained by killing 95% of adults only during the 1 or 2 years preceding the onset of outbreaks (Figure 13). The onset of outbreaks can be predicted through yearly surveys. Although this result was unexpected, it reflects the general situation with direct control of destructive bark beetles. During epidemics, generation survival tends to be high, and unless very high proportions of the beetles are destroyed, damage levels will remain substantial.

Since this model is conceptual in structure and formulation, caution must be exercised in interpreting simulated results. The reliability of predictions based on the model would be significantly improved by the following changes: (a) the revision of the forest model to include height and dbh distribution of spruce as functions of site quality and stand age; (b) testing and refinement of the windthrow submodel; and (c) testing and refinement of the tree susceptibility submodel. Nevertheless, the model in its present form is useful for exploring various aspects of host-insect interactions, and possible beetle population and tree mortality consequences of forest management practices and control by killing adult beetles.

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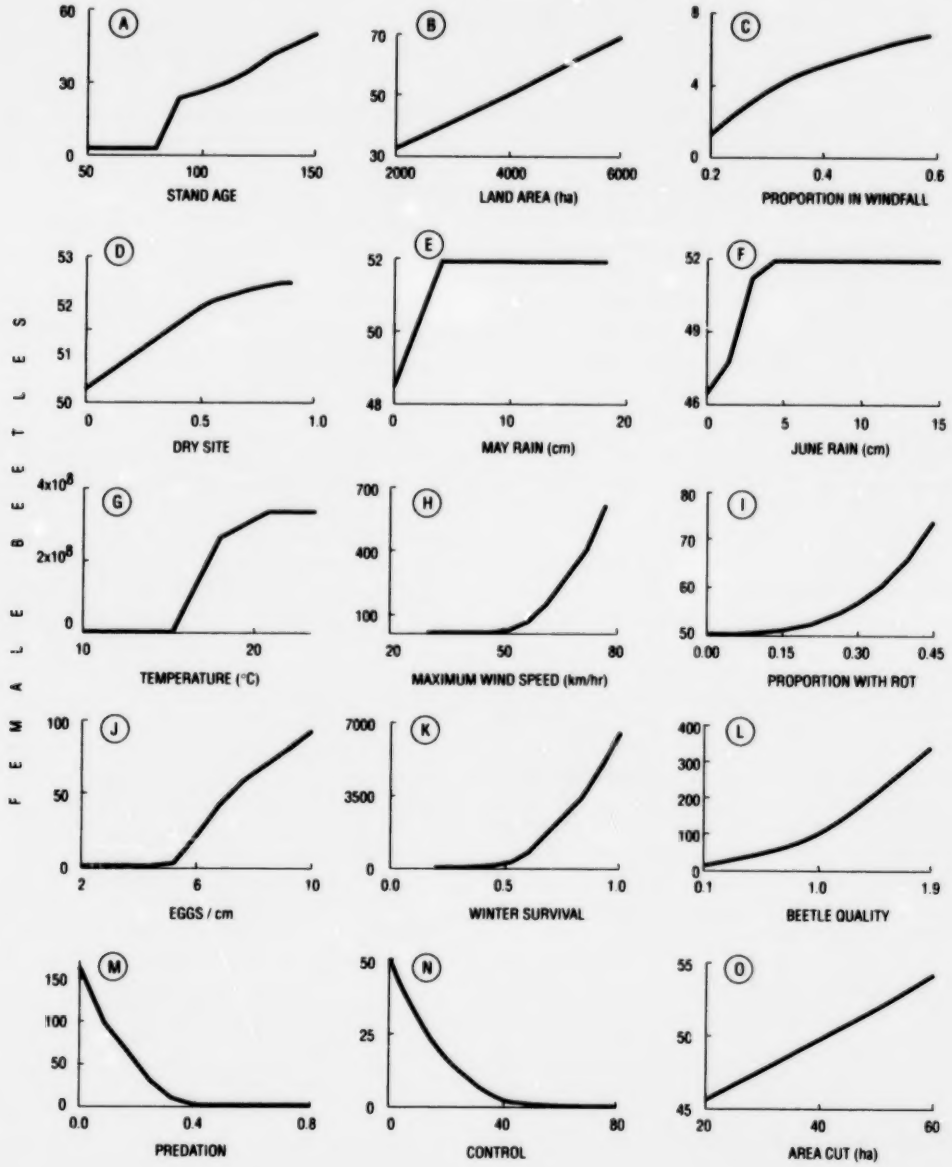


Figure 15. Parameter sensitivity output. Variables are:

(i) The total number of female beetles produced.

(ii) The cumulative mortality of trees over the 20 year run. Both variables are graphed on the vertical axis. The parameters which were used in this analysis were:

(A) STAND AGE - age of the stand at the initiation of the simulation (default = 100 years)

(B) LAND AREA - area of the stand (default = 4000 ha)

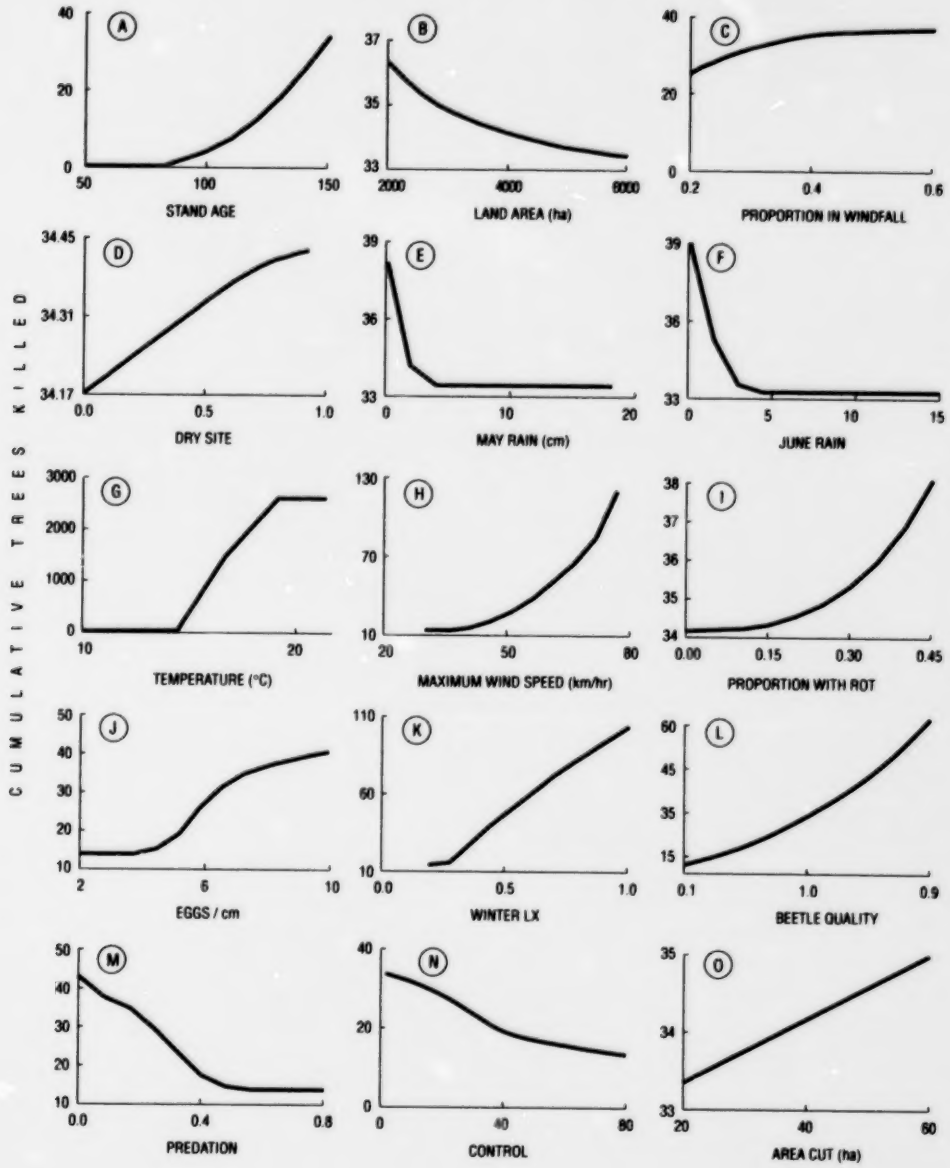
(C) PROPORTION IN WINDFALL - proportion of beetles attacking windfall (default = 0.4)

(D) DRY SITE - proportion of area that is a dry site (default = 0.0)

(E) MAY RAIN - amount of rain in May (default = 10 cm).

(F) JUNE RAIN - rainfall in June (default = 8 cm)

(G) TEMPERATURE - Mean temperature in July and August (default = 10°C)



(H) MAXIMUM WIND SPEED - default = 50 km/hr
(I) PROPORTION WITH ROT - proportion of trees with visible decay (default = 0.0)
(J) EGGS PER CM - eggs per centimetre of egg gallery (default = 7.0)
(K) WINTER SURVIVAL - proportion of beetles that survive the winter
(L) BEETLE QUALITY - numerical index of beetle vigor (default = 1.0; range 0.1 - 1.9)
(M) PREDATION - proportion of beetles killed from woodpecker predation
(N) CONTROL - Percentage of adult beetles killed through direct control (default = 0.0)
(O) AREA CUT - Area of spruce forest cut each year (default = 0.0 ha)